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Macroevolution of Bold Color Patterns Across Teleostean Fishes

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MACROEVOLUTION OF BOLD COLOR PATTERNS ACROSS TELEOSTEAN FISHES

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ABSTRACT

Fishes include some of the most visually striking vertebrate radiations and have repeatedly evolved bold color patterns, including bars, stripes, and spots. Such strong color patterns are hypothesized to provide multiple functions, including avoiding predation by obscuring recognizable features and communicating with others to secure territories and mates. Despite increasing focus on the functions and proximate drivers of color pattern evolution, the relevance of such pressures across broad taxonomic and time scales remain much less resolved. Using over 5000 species within the largest vertebrate radiation, teleostean fishes, I employ phylogenetic comparative methods to explore the lability and potential coevolutionary relationships between color pattern traits and habitat. Evolutionary models reveal that pattern traits are labile across fishes and transitions most often occur between patternless and non-contrast pattern species. I also find support for the long-held belief that reef fishes are more patterned than their non reef-dwelling marine relatives. Given the marked diversity of body shapes within this group and proposed functional relationships between fish body depth and stripe orientation on the body, I also test for relationships between color pattern types and body shape. I find differences in body shapes between species with singular versus repeating patterns, such as single and multiple stripes, suggesting potential coevolution of color pattern and morphology over macroevolutionary scales. This study is a key step towards uncovering the story behind the persistence of bold color patterns in nature and provides insight into how evolutionary pressures shape color displays across deep time.

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TABLE OF CONTENTS

Table of Contents (Continued)

Page

LIST OF TABLES

Chapter 1

Table Page

Chapter 2

Table

LIST OF FIGURES

Chapter 1

Figure Page

Chapter 2

Figure

CHAPTER 1

The Evolution of Bold Color Pattern Diversity

INTRODUCTION

High contrast color patterns, such as bars, stripes, and spots, generate some of the most visually striking displays in nature. These markings have evolved repeatedly across the tree of life within groups as diverse as mammals, plants, insects, and fishes and remain a popular topic for scientific study as well as TV shows and books aimed at the general public (Attenborough's Life in Colour n.d.). Methodological advances and interdisciplinary collaborations are bringing us ever closer to answering how and why we see such vivid displays in nature (Cuthill et al. 2017). While we continue to make advances in understanding genetic underpinnings, developmental mechanisms, and ecological functions of bold color patterns, few studies have investigated how they have evolved over macroevolutionary timescales. A macroevolutionary perspective enables us to compare the evolutionary lability of pattern types, identify potential coevolution between one pattern type and another or habitat, and use the comparative method to identify potential adaptive evolution, thereby providing insight into the evolutionary pressures acting over deep time.

Bold patterns are hypothesized to serve several functions, including communication and crypsis, sometimes simultaneously. Visual communication receivers can be a member of

the same species: color patterns are linked to social communication (Caro et al. 2017) and can signal territorial information to rivals and indicate fitness to potential mates (Lorenz 1962). Patterns can also serve as an effective warning signal to other species: many toxic species use bright warning patterns, or aposematism, to advertise their unpalatability including poison frogs and terrestrial carnivores (Stankowich et al. 2011). The strategy is effective enough for the warning color patterns to evolve in harmless species, resulting in a dishonest signal known as Batesian mimicry (Bates 1981; Davis Rabosky et al. 2016). Another example of anti-predator color patterns are strong markings, such as an eyespots, which can be used to intimidate or startle an attacker (Kjernsmo et al. 2016). Bold patterns can also be used to avoid detection (crypsis). Usually we think of crypsis as being achieved through background matching, which conjures up images of motionless animals camouflaged against a static background (Grant and Howlett 1988). However, some types of contrast pattern can also function as cryptic coloration: the high contrast color margins of bar (vertical lines), stripe (horizontal lines), and blotch patterns are hypothesized to visually break up a body outline, rendering the individual unrecognizable (Schaefer and Stobbe 2006; Stevens et al. 2006; Webster et al. 2013). This disruption of shape via contrast patterns is known as disruptive coloration and is hypothesized to work most effectively against a visually complex background (Price et al. 2019a). Even if an animal must move, bold colors may still be advantageous towards reducing predation by slowing recognition times (Hall et al. 2013).These strategies may result in the evolutionary persistence of bold patterns across clades, especially in visually complex habitats such as reefs.

Teleostean fishes are a highly diverse group representing over half of extant vertebrate diversity and are an ideal group for investigating color pattern evolution. Fishes, and those that inhabit reefs in particular, exhibit an astounding array of patterns and colors (Nelson et al. 2016). Moreover, fish have the largest number of pigment types within vertebrates (Salis et al. 2019) and the genetic and developmental basis of patterning is being established through the use of zebrafish, a model organism for genetics, which (as their name suggests) have dark stripes (McCluskey et al. 2021; Parichy 2021). We know fish species can discern varying degrees of patterning, (Siebeck 2004; Siebeck et al. 2008; Marshall et al. 2019), even with limited acuity or within reduced lighting environments (Endler 1992; Barry and Hawryshyn 1999). This ability to discern color pattern signals likely make both inter and intraspecific communication and crypsis relevant evolutionary pressures. Teleosts also exhibit an astounding array of ecologies and morphologies, ranging from benthic elongated forms to bullet-shaped open water swimmers to fruit-eating oversized piranha relatives and inhabit a wide range of habitat types, from pelagic waters to the structurally complex coral reefs. Similar to tigers blending into a forest, fishes, such as the humbug damselfish, may use bold barred patterns to remain undetected against the visually complex corals (Cott 1940; Phillips et al. 2017).

Some markings are thought to functionally complement one another. Markings that cross the margin of the eye are thought to help disguise the vulnerable head-region (Cott 1940; Barlow 1972), while concentric rings, or eye spots' may mimic the eye of a larger animal (Stevens 2005). This is thought to be intimidating and visually distracting to predators

(Neudecker 1989). Within butterflyfishes Kelley and colleagues found that while eye bars are conserved within butterflyfishes, consistent with the literature supporting the concealing of vulnerable and recognizable eye outlines via visual disruption, eyespots, which were expected to coevolve with eye concealment, are relatively evolutionarily labile (Kelley et al. 2013) A more recent study surveying multiple reef fish families found eyespots were present in closely related species, suggesting evolutionary conservatism, though their location on the body may relate to different habitats in the water column (Hemingson et al. 2021).

The connection between habitat complexity and bold pattern in fishes has been a prevailing idea within the literature and is consistent with the expectation that disruptive coloration works best in complex environments (Merilaita 2003). Unsurprisingly, most attention has been focused on reef fishes (Lorenz 1962; Gaither et al. 2020). It has been argued our perception of reef fish diversity may be primarily driven by the dazzling array of colors and patterns (Bellwood 1996). Lorenz hypothesized that these so-called 'poster colored' bright displays play an important role in intraspecific communication, specifically antagonistic interactions such as competition over territory and mates (Lorenz 1962). While it is still not known if reef fishes are especially diverse in terms of their color patterns relative to fishes living in other less complex habitats, it has been demonstrated that strong bar patterns are associated with complex rocky or vegetation-heavy substrates in freshwater African cichlid radiations, and may drive convergence in rocky bottom-dwelling stream fishes (Armbruster and Page 1996; Seehausen et al. 1999).

As we continue to strengthen our knowledge of proximal factors influencing the adaptive significance of these traits, it is important to explore these questions at a large scale to gain a comprehensive understanding of color pattern diversity over time. Macroevolutionary studies of color pattern evolution are few and far between: mammals (Stankowich et al. 2011), insects (Tan et al. 2017), squamates (Chen et al. 2012) and fishes (Alfaro et al. 2019). With an ever increasingly resolved fish Tree of Life, a macroevolutionary investigation of the color pattern types at much larger scales is now possible. We investigate the overall pattern evolution within 5197 species of teleost from both marine and freshwater environments. We break down bold patterns on the head and body of teleost fishes into 14 sub-elements and, using the teleost phylogeny from(Rabosky et al. 2018) quantify the broad scale patterns of bold color pattern evolution across teleost fishes. Specifically, we investigate 1) the relative evolutionary lability of color pattern types, 2) coevolution between pattern elements, and 3) coevolution between reef habitats and color patterns.

METHODS

Image Data Collection

We collected lateral photographs of 6000+ species of teleost fishes at the Smithsonian Museum of Natural History; See (Price et al. 2019b) for details. Digital images were taken of 1-3 specimens per species with a Nikon D7200 SLR camera with 60mm macro

lenses on a tripod system under controlled lighting conditions within the museum. All images represented the lateral view of preserved specimens submerged in ethanol. These images were used to score presence/absence of color pattern elements for each species. Species were matched to the Rabosky phylogeny resulting in a dataset of 5171 species which was used for all subsequent analyses. Data from Fishbase on presence/absence of reef habitat for marine species was used for analyses of coevolutionary relationships between color pattern and habitat; See (Larouche et al. 2020).

Scoring Color Patterns

Scoring color patterns by categories is a feasible way to study the color pattern continuum found in nature (Salis et al. 2019). Though there is no current universal set of patterning traits in the literature, there are comparable pattern types across most organisms, including linear patterns like bars (vertical lines) and stripes (horizontal lines), conspicuous markings such as eye spots, lines and saddles, and full body motifs such as mottled or reticulated markings. Color pattern traits are modeled after previous animal color pattern studies, including some in fishes, and modified to apply to the range of patterns observed across teleosts (Kelley et al. 2013; Halperin et al. 2017). A total of 14 traits were scored for presence or absence, for each species, based on up to three specimens per species. To test for scoring consistency, pattern traits were scored in two rounds for a randomized list of 50 species pulled from eight major reef fish families: Acanthuridae, Chaetodontidae, Haemulidae, Lutjanidae, Mullidae, Pomacanthidae,

Pomacentridae, and Siganidae (Figure 1). Different combinations of these traits were used to generate broader categories; For example, to create the pattern trait ‘all eye marks’ species who had either an eye stripe, eye bar, or other eye marking were scored present for ‘all eye marks’ (Figure 2).

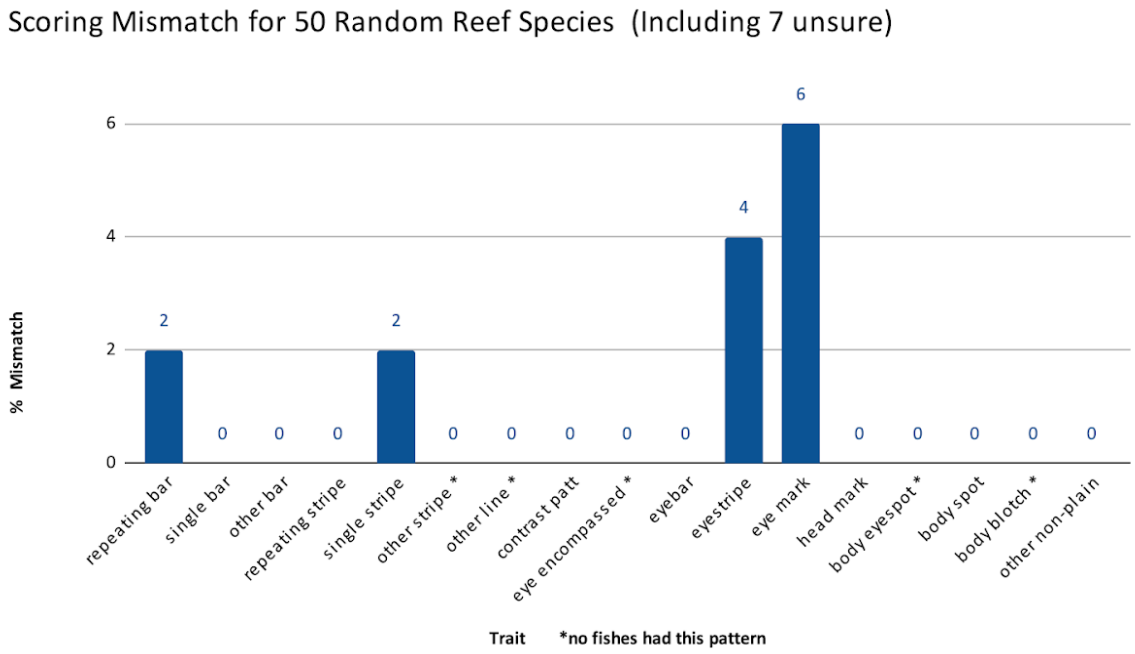


Figure 1: Presence/absence scores for 50 species from 8 reef fish families were scored twice and mismatches in scores were compared. Species names were assigned a random character string by an individual other than the scorer to avoid any scoring bias based on species name recognition. An unsure category was included for patterns that were unclear, but these species were included in this comparison.

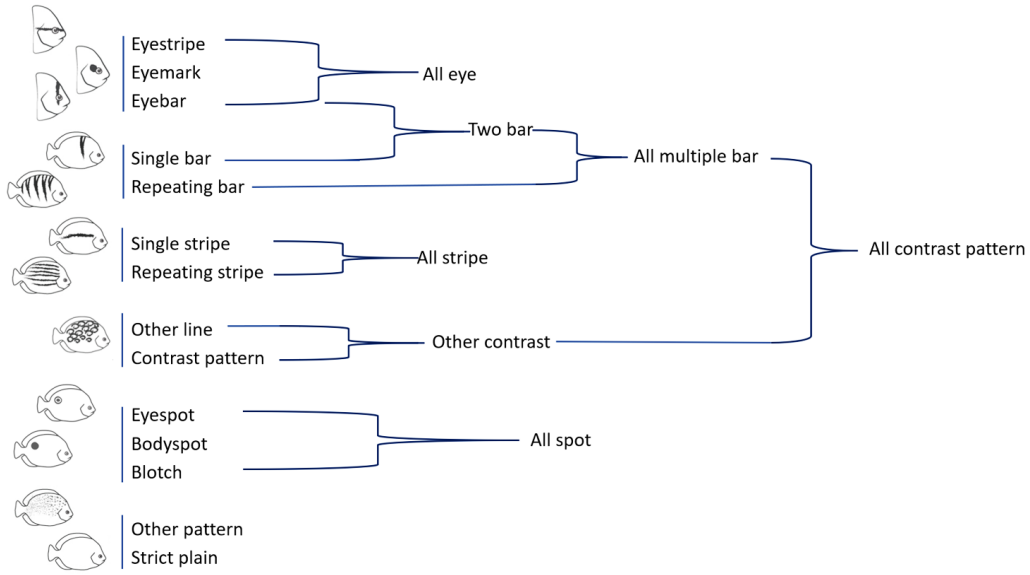


Figure 2: Presence/absence scores for species were used to create combination traits representing different groupings of color pattern types.

Contrasting color patterns are well documented in adult fish, and to address any potential issues caused by ontogenetic color changes, only the three largest (mature) specimens were photographed and used to score color patterns per species. Some families are known to exhibit considerable sexual dimorphism in color pattern expression. To account for species where strong sexual selection may be driving color displays, scores for the groups Labridae, Cichlidae, Mullidae, Monacanthidae, and Pleuronectiformes were supplemented with species descriptions and alternate photo records of female individuals from the literature. In addition, any notable variability in patterning between specimens was flagged and checked against supplementary resources.

Testing for Pattern Preservation

Some specimens fade after capture and preservation (Netto-Ferreira and Luckenbill 2016), creating potential bias towards detecting less pattern traits. To test for reliability of using preserved specimen photos to score species for color pattern categorizations, we compared pattern scores from a test version of our preserved fish photo dataset containing 71 species across same reef families as used above to scores recorded from living fishes provided by Carlos and Allison Estape from their Photoshelter image gallery: https://carlosestape.photoshelter.com/. Live images were supplemented with the Smithsonian Museum of Natural History's online live fish photobase for use in this comparison test. For the scoring of the final dataset, patterns were conservatively scored as 'present' for each element and species with uncertainty were checked against supplementary resources. Contingency table analyses (Figure 3) revealed an average percent match of presence/absence scoring of 7.3%. Low error percentages between live, at depth photos for traits used in our analyses indicated color patterns scores from live fish are comparable to those from preserved fish specimens although we want to be cautious interpreting eye-stripes.

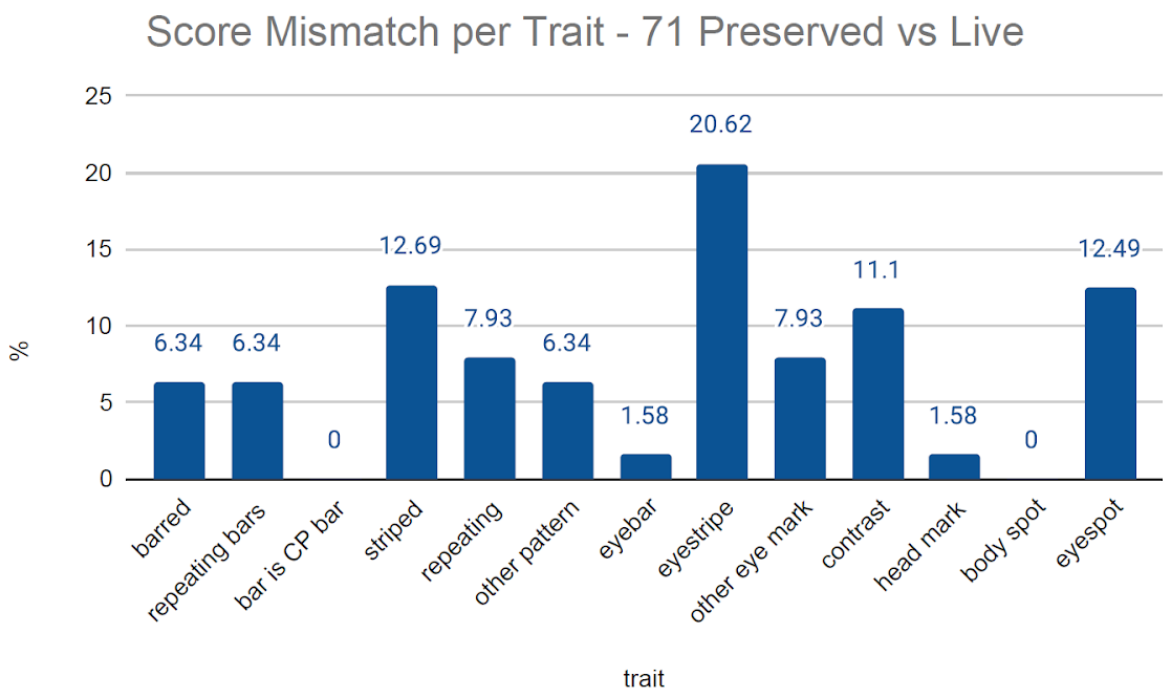


Figure 3: Presence/absence scores for 71 species from 8 reef fish families were scored for preserved fish photos and photos of live individuals at depth. Mismatches in scores were compared.

Estimating Lability of Color Patterns

To test if some pattern traits, such as bars, stripes, and spots, are more labile than others, such as eye-concealing marks, we estimated the phylogenetic signal, which is the statistical dependence between traits and the phylogeny. We estimated the strength of phylogenetic signal in our binary traits using the D statistic, a sum of the estimate of the number of changes in a binary trait across the nodes of a phylogeny based on the observed tip values (Fritz and Purvis 2010). Few trait changes, and thus high

phylogenetic signal, result in a D of 0 while many switches, or low signal and high lability, result in D values closer to 1. This D value is then compared to a D value from 1) a simulated brownian motion (high signal) model and a random (low signal) model, resulting in two p values. Traits with conservative estimates suggest stabilizing selection or slow evolutionary rates, and labile estimates suggest rapid change driven by other processes such as ecological pressures, sexual selection, or release of selective constraints (Revell et al. 2008). We implemented the analyses using the function phylo.d in the R package Caper (Orme n.d.) with the teleost phylogeny (Rabosky et al. 2018).

In addition, color pattern data was mapped onto the phylogeny using Stochastic character mapping in SIMMAP (Bollback 2006) to visualize color pattern trait clustering and estimate the number, timing, and pathway of the transformations between pattern types. Stochastic character mapping implements continuous time Markov models for discrete traits in a Bayesian framework and is preferred over maximum likelihood and parsimony methods of ancestral state reconstruction because it takes into account uncertainty in the reconstruction. It also provides another way to infer lability, by examining the transition rates and determining if patterns are lost or gained at equal, faster or slower rates. I ran 1000 iterations with an equal rates prior on the Q matrix and branch length prior on the scaled phylogeny from Rabosky et al. and performed stochastic mapping on four sets of binary traits: 1) eye traits, which include combined eye stripe, eye bar, other eye marks (1) versus all others (0), 2) bar traits, which include combined single bar, multiple bar, marks (1) versus all others (0), 3) stripe traits, which include combined single stripe, multiple stripe marks (1) versus all others (0), and 4) contrast patterns, which include

combined single bar, multiple bar, single stripe, multiple stripe, other line or blotched patterns (1), versus non high-contrast patterns and all others (0).

Testing for Coevolution between eye obfuscation and body spot patterns

We tested for correlated evolution between eye-obfuscation marks and body spots in teleosts using the function fitPagel (Pagel 1994) in Phytools (Revell 2012) in R (R Core Team 2020). The combined trait 'all eye marks', consisting of combined eye stripe, eye bar, other eye marks (1) versus all others (0) was compared to the presence/absence of the combined trait 'all spot' consisting of combined body spot, body blotch, and body eyespot (1) versus all others (0). Using only the eyespot category was not feasible due to the low number of eyespot occurrences.

Testing for coevolution between contrast patterns and reef habitat

Tests for coevolution between pattern types and habitat were performed in the same manner as above on a subset of the data: marine species only. The presence/absence of reef habitat was compared to the presence/absence of the following pattern traits in turn: 1) multiple bars (1), versus all others (0), 2) multiple stripes (1), versus all other (0), 3) eye traits, which include combined eye stripe, eye bar, other eye marks (1) versus all others, and 4) contrast patterns, which include combined single bar, multiple bar, single

stripe, multiple stripe, other line or blotched patterns (1), versus non high-contrast patterns and all others (0).

It is important to acknowledge that these methods to identify phylogenetic correlations between binary traits are influenced by issues of pseudoreplication (Maddison and FitzJohn 2015): a single evolutionary event can drive the identification of a significant association. For each of the pattern traits tested we confirmed that there were multiple independent evolutionary transitions from our stochastic character maps, although philosophically it may be hard to determine how many independent origins are necessary to prove a correlation (Maddison and FitzJohn 2015). In addition to these tests in marine fishes, we also tested for the coevolution of single stripes (single stripe =1 versus all else =0) and freshwater habitats (freshwater=1 versus reef and non-reef=0) due to the difference in the occurrence numbers of single stripes species in freshwater (147 species) versus marine (40 species) habitats.

RESULTS

Lability of Color Patterns

All color pattern traits tested showed intermediate phylogenetic signal strengths, which were significantly weaker than the expectation under a threshold Brownian motion (BM) model and stronger than the random expectation (Table 1). Pattern traits bars, stripes, other contrast patterns, spots, and plain all had a probability of 0 that the observed signal

resulted from random and BM processes across the phylogeny. Eye traits were similar except the probability of the eyemark signal resulting from a BM process was 0.001 instead of 0. These results indicate that bold pattern types are fairly evolutionarily labile but there is still some phylogenetic pattern within them. Differences in lability between traits were small, although eye marks had the lowest D value indicating they may be slightly more evolutionarily conserved than other pattern traits. Overall, bar and stripe traits have evolved independently multiple times across the teleost tree, and multiple bars are far more numerous than single bars, while single stripes are more numerous than multiple stripes (Figure 4).

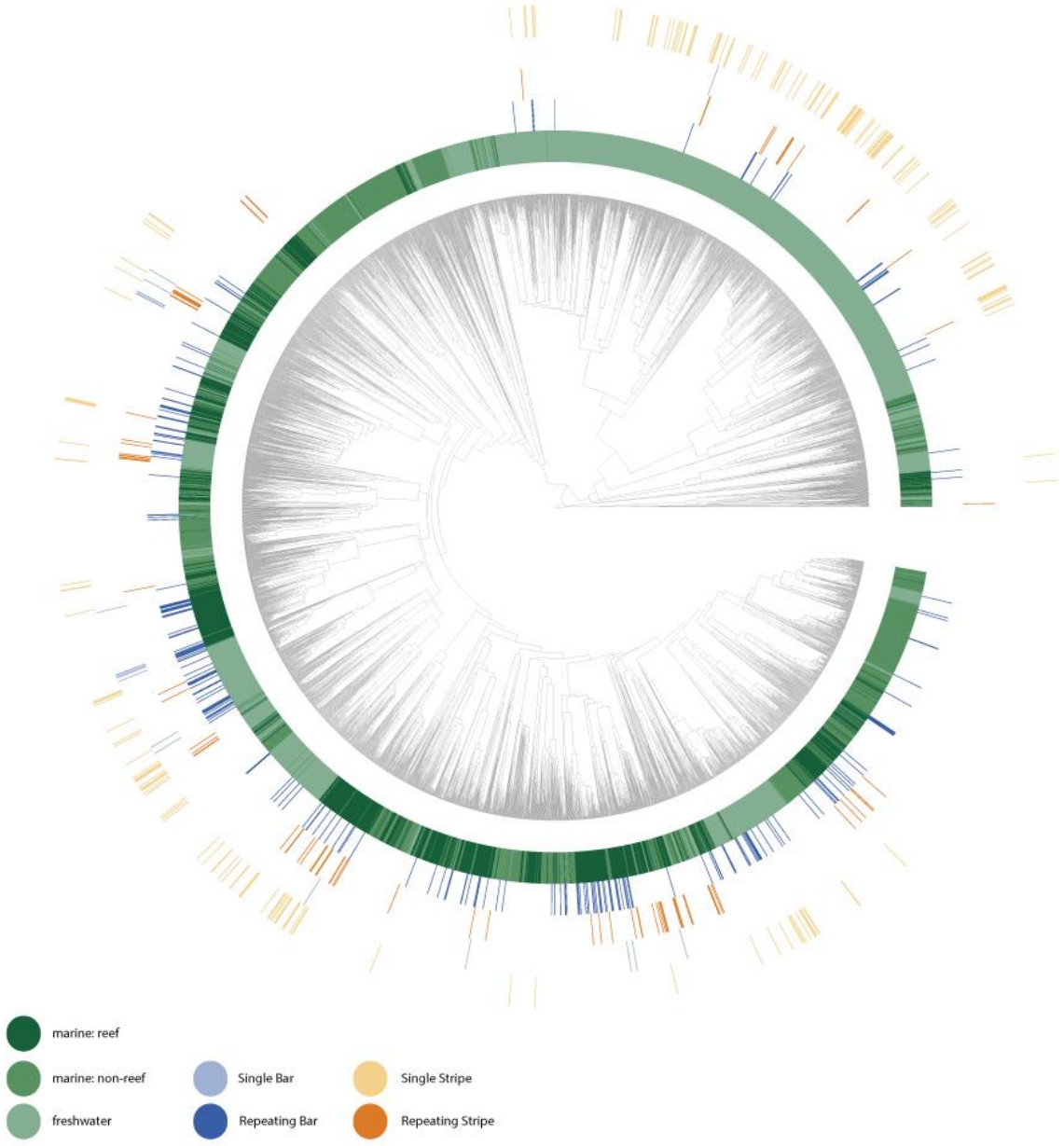


Figure 4: Presence/absence of multiple stripes (orange), single stripes (yellow), single bars (light blue), and multiple bars (dark blue), and habitat mapped on the teleost phylogeny.

Trait grouping	Estimated D (marine + freshwater)	p-value (BM model)	p-value (Random model)
All bars	0.5058769	<0.0001	<0.0001
All stripes	0.5282991	<0.0001	<0.0001
All contrast patterns	0.514357	<0.0001	<0.0001
All spots	0.5839986	<0.0001	<0.0001
All eye	0.2922535	<0.0001	<0.05
Plain	0.4160337	<0.0001	<0.0001

Table 1: Phylogenetic signal (estimated D) values for color pattern traits with 1 indicating high signal (low evolvability) and 0 indicating low signal (evolvable). P values indicate the probability the D value estimated from the observed data differs from either a Brownian Motion (random evolutionary walk) model or a random distribution of the trait states on the tips.

Transition estimates between pattern trait states for trait set 4 (contrast patterns) revealed the highest number of transitions from plain to non-contrast patterns (510 transitions), followed by the opposite: loss of non-contrast pattern back to the plain state, and then

transitions from non-contrast patterns to non-bar/stripe contrast patterns (510, 240, 111 transitions respectively) (Figure 5A). Overall, transitions are between non-contrast patterns and plain, and are scarce between bar and stripe traits. Similarly, eye traits show high transitions from plain into pattern traits eye bar, eye stripe, and other eye marks, but transitions were comparatively low between eye stripes and eye bars (Figure 5B).

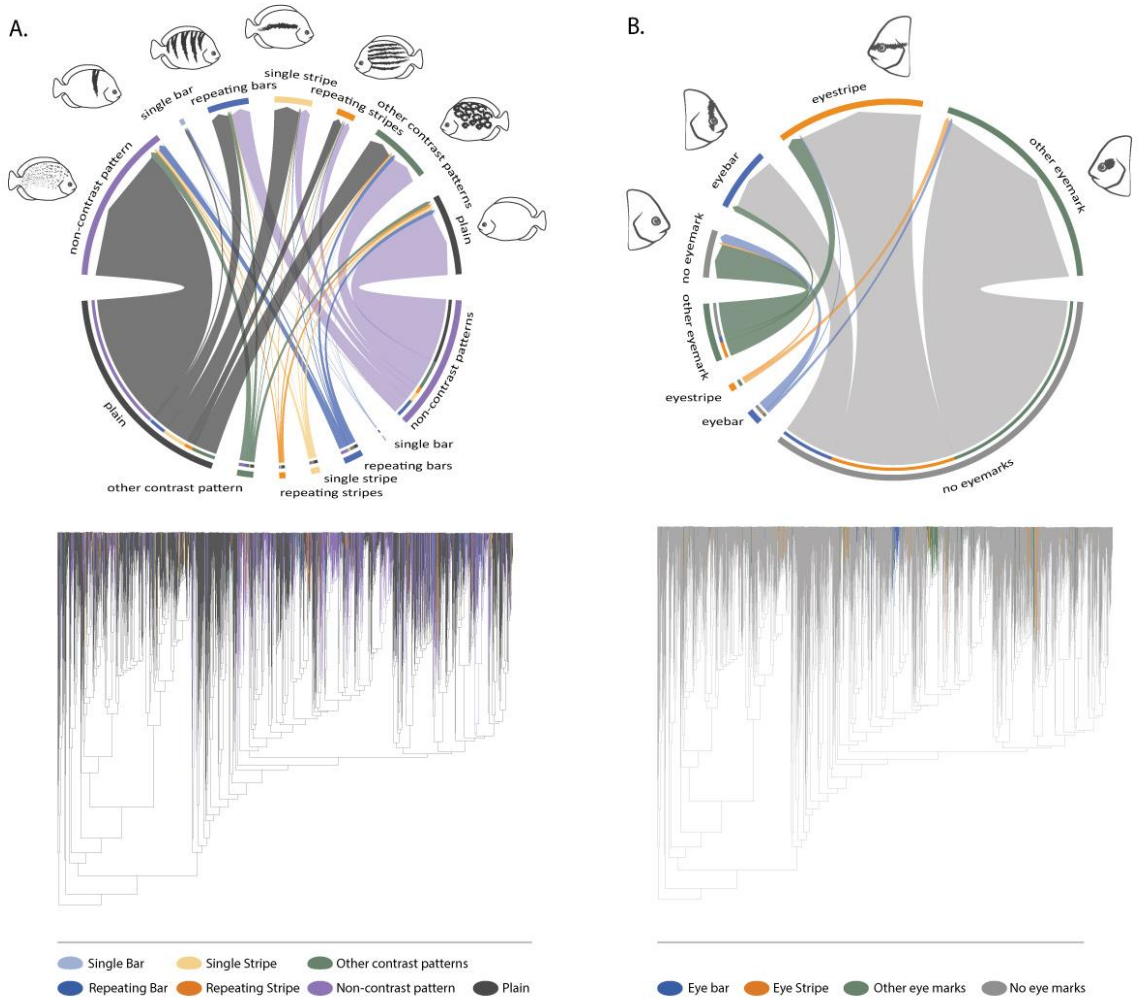


Figure 5: average number of transitions between trait states over 1000 iterations in SIMMAP shown by cord diagrams (top) and across the teleost phylogeny (bottom) for trait set 4 consisting of seven contrast pattern traits (A) and trait set 1 consisting of four eye traits (B).

Coevolution between eye obfuscation and body spot patterns

We find support for coevolutionary relationships between all eye marks (eye bars, stripes, or marks) and body spots (body spot, blotch, or eyespot) ($p<0.05$, ΔAIC 9.09). We also see a similar result when all eye marks are tested for coevolution with the combined trait contrast patterns (bars, stripes, and other contrast patterns) ($p<0.05$, ΔAIC 539.98) (Table 2).

Pattern trait	**Model**	**P value**	**ΔAIC**	**Akaike weight**
Eye-Spot	independent	<0.05	9.09	0.01
	dependent		0	0.99
Eye-Pattern	independent	<0.05	539.98	5.57e-118
	dependent		0	1

Table 2: fit.Pagel (Phytools) tests for coevolution between binary traits eye marks and 1) body spots and 2) all combined contrast patterns in teleosts.

Coevolution between contrast patterns and reef habitat

We find strong support for the coevolutionary model over an independent evolution model for reef habitats and bold color pattern traits. Across marine teleosts, models supported coevolution between reefs and the pattern types multiple bar (p=7.54e-13, ΔAIC 51.83), multiple stripe (p=8.18e-11, ΔAIC 223.07), eye markings (p=7.22e-28, ΔAIC 120.99), and a combined trait of contrast patterns (p=8.46e-32, ΔAIC 139.09). For all pattern elements tested, the transition rate (Q) matrices revealed consistently higher rates of the gain of color pattern traits when the initial state included reef habitat, and lower rates of losing pattern traits when the initial state included reef habitat (Figure 6). The opposite relationships was found when comparing the independent and coevolution model for non-patterned (i.e. plain) species (p=4.78e-34, ΔAIC 149.4) with the directionality of the transition rate matrix indicating plain fishes are more likely to gain pattern when moving from non- reef to reef habitats and, conversely, are more likely to lose pattern when transitioning to non-reef habitats (Figure 6).

Multiple Bars

	0|0	0|1	1|0	1|1
0|0	-1.932358	1.115198	0.817160	0.000000
0|1	3.292629	-5.808048	0.000000	2.515419
1|0	78.016397	0.000000	-79.131595	1.115198
1|1	0.000000	26.704498	3.292629	-29.997127

Eye Marks

	0|0	0|1	1|0	1|1
0|0	-1.313481	1.164756	0.148725	0.000000
0|1	3.233916	-5.733260	0.000000	2.499344
1|0	24.164279	0.000000	-25.329035	1.164756
1|1	0.000000	10.584313	3.233916	-13.818230

Multiple Stripes

	0|0	0|1	1|0	1|1
0|0	-1.097918	1.063463	0.034455	0.000000
0|1	3.349406	-4.187301	0.000000	0.837895
1|0	75.105612	0.000000	-76.169075	1.063463
1|1	0.000000	18.983456	3.349406	-22.332861

All contrast patterns

	0|0	0|1	1|0	1|1
0|0	-2.781718	1.138336	1.643382	0.000000
0|1	3.266973	-8.476112	0.000000	5.209139
1|0	36.743187	0.000000	-37.881523	1.138336
1|1	0.000000	14.001753	3.266973	-17.268726

Figure 6: Dependent model rate (Q) matrices showing transition rates based on habitat (reef=1, non-reef=0) all with a $p<0.05$.

DISCUSSION

Lability of Color Patterns

Our study includes over 5000 species of teleost fishes across 400 families, making it the first study of broad scale trends in color pattern evolution within any clade of animals. We find that high contrasting color patterns such as bars, stripes, spots, are not strongly conserved phylogenetically and are thus relatively evolutionarily labile. The evolutionary flexibility we observe may be facilitated by the regulation of pigment producing genes. In some cases, only a few genes need to be turned on to produce a pattern, such as the

expression of contrasting bars (Hulsey et al. 2018). Pigment cells can also interact with one another, which can either promote or inhibit pigment presence and migration across the skin (Parichy 2021). One of the most well known of these mechanisms is the reaction-diffusion theory, where cells chemically promote or inhibit one another through passive feedback loops. This autonomous process can occur throughout morphogenesis, and is known as the Turing model (Turing 1990). As a fish grows, pigment cells can promote or inhibit one another to form even patterns, including reticulate patterns on pufferfishes or repeating stripes on angelfishes that increase in number to maintain spacing as a fish increases in size (Kondo and Asal 1995). These mathematical models may explain why some bold patterns are observed in fishes and other animals (Scarabotti et al. 2020). Other pattern types may be influenced by development: juvenile clownfishes gain white bars from anterior to posterior, while bar expression in adults is lost evolutionarily in the opposite order (Salis et al. 2018). Patterns can also be changed by species hybridization, which has been linked to rapid evolutionary changes in reticulate-type patterns expressed in pufferfishes (Miyazawa, 2020).

Stochastic character mapping revealed that the highest rates of transition were from plain to non-contrast patterns, and transitions between bar and stripe traits were comparatively scarce. The lack of transitions between bars and stripes suggests that, while pattern types may be labile overall, underlying mechanisms, such as those governing pigment cell expression and migration, may impose some restrictions on lability between pattern types

of differing orientations on the body. While mammals possess melanocytes which are responsible for dark pigmentation, fishes have a more diverse set of color cells (Salis et al. 2019). These include melanophores, cells containing dark pigments, erythrophores, cells containing red carotenoids, xanthophores, cells containing yellow carotenoids, and iridophores, cells that reflect light and create silvery effects (Kelsh 2004). In addition, mammal pigment cells exhibit dorsolateral cell migration, chromatoblast migration in zebrafish is known to vary by pigment type: xanthoblasts can move dorsolaterally, iridoblasts can migrate along the medial pathway, and melanoblasts can do both (Milos and Dingle 1978; Raible and Eisen 1994; Parichy et al. 2000). These differing migratory patterns, in addition to the aforementioned chromatophore interactions across ontogeny, could contribute to the variation we observe in transition ease between contrast pattern types in teleosts.

The overall signature of patterns we detect across teleosts may be due to a mix of ecological functions and adaptive pressures, including communication (Guthrie and Muntz 1993) and crypsis (Cott 1940). Fishes can distinguish colors and patterns rather well, and some reef fishes can distinguish varying degrees of color (Siebeck et al. 2008). Contrasting stripes in particular are used to signal parasite cleaning services (Stummer et al. 2004) and have been linked to schooling and aggregating behaviors (Seehausen et al. 1999; Negro et al. 2020). Bold pattern types are also used to attract the attention of potential mates. Sexual selection can also influence the evolution of bright patterns

(Lorenz 1962) and pattern arrangements (Chen et al. 2012); contrary to expectations of natural selection, some animals increase the contrast of their patterns to become more conspicuous against the background than their conspecifics (Marchetti 1993). Additionally, color patterns in butterflyfishes show more rapid evolution in recent lineages and indicate speciation processes may overshadow ecological pressures, especially in lineages close in geographical space (Alfaro et al. 2019).

While bold patterns can help animals stand out, they can also function as an anti-recognition strategy. Disruptive color markings create bold visual contours within a shape, and can break up the recognizable pupil, obscuring an eye, or may be present across thes body, breaking up the entire body shape outline against a background (Stevens and Merilaita 2009b). In this way, disruptive markings can function as a type of crypsis and disguise individuals from recognition (Gomez and Théry 2007; Marshall and Gluckman 2015). Some reef fish species, such as the humbug damselfish, are known to use this disruptive strategy (Cott 1940; Phillips et al. 2017). Bold color patterns are most likely influenced by varying combinations of natural and sexual selection. It is important to note that we scored our fish based on how they look in even lighting without a background, but light attenuation from a top down source, receiver distance, and the acuity of the viewer may make some strong, seemingly obvious patterns cryptic against the complex backdrop of the reef (Siebeck et al. 2008,Stevens and Merilaita 2009a). Orientation of the body as a fish swims may also interact with the appearance of color patterns to create different effects during swimming (Denton and Rowe 1998). We also

acknowledge that some patterns, such as UV and fin markings that may function as communication signals in some groups (Siebeck 2004), were not addressed in this study. Instead, we focus on patterns consistently displayed on the body of the fish. Future studies from the perspective of the signaller and receiver can help illuminate the functions behind specific color arrangements, especially in different environments (Cheney 2018).

Coevolution between eye obfuscation and body spot patterns

Some trait combinations, such as eye-obfuscation markings and eyespots on the body, might work especially well in conjunction with each other. Eye lines are thought to obscure recognition, concealing of vulnerable and recognizable eye outlines via visual disruption while eye spots (a spot with a concentric ring) may serve instead as an intimidating false large eye (Cope 1890; Stevens 2005) or distraction (Neudecker 1989; Kjernsmo et al. 2016; Kang et al. 2017), further drawing attention from the true eye and resulting in a more effective anti-predator defense. Though not statistically significant, Kelley and collaborators observed that butterflyfish species with eyespots also had vertical eye bars (Kelley et al. 2013) and a similar trend was observed in cusk eels (Uiblein and Nielsen 2005; Kelley et al. 2013). Our tests find strong support for the coevolution model over the independent evolution model for eye marks and general body spots (with or without the concentric ring) within teleosts, supporting the idea that these color markings may work in tandem. Previous findings that eye spots marks evolved

more recently than eye marks and are therefore less evolutionarily labile (Kelley et al. 2013) were supported by our findings of eyemarks having slightly higher phylogenetic signal than spot marks in teleosts. Due to our sampling within cheatodontids, we did not have the power to test just within this group, and color patterns may experience varying degrees of evolutionary pressures based on taxonomy or phylogenetic scale.

We also find support for a coevolutionary relationship between eye marks and any of the body contrast patterns, indicating that eye makers could be a continuation of the disruptive function of contrast pattern (Barlow 1972). One reason that this could be effective is that the eye is a telltale sign for recognition, thus, obscuring the eye plus a body disruption pattern could be a really effective way to break up easily recognizable features. Indeed many fish with disruptive patterns seem to have them across most of the body, and in some cases the pattern is evenly repeated across the entire fish.

Coevolution between contrast patterns and reef habitat

Coral reef fishes have long been associated with bright, diverse, and bold color patterns (Lorenz 1962), but until now this has not been explicitly tested. We find that marine teleost species with contrast stripe, bar and blotch patterns coevolve with structurally complex reef habitats, supporting the assumption that reef fishes are more boldly patterned. Our findings are consistent with the hypothesis of shape disruption, as disruptive color patterns are hypothesized to work most effectively against visually

complex backgrounds (Tan et al. 2017,Price et al. 2019a). Shape disruption would likely be an equally effective strategy in comparably complex freshwater habitats, such as planted lake bottoms, in addition to murky waters where acuity can already aid in reduced visual detection (Caves et al. 2018), though some bold patterns, such as those found within corydora catfishes, have also been proposed to be aposematic (Harris and Jenner 2019). Another potential explanation is the higher need for nuanced communication and territorial interactions facilitated by pattern-based communication. Lorenz proposed that these seemingly flashy 'poster colored' displays may help reef-dwelling species communicate with conspecifics in this busy and crowded environment as they stake out and defend territories and locate potential mates (Lorenz 1962).

Conclusion

We show reef fish are truly the eye-catching patterned group we had long thought, and that bold color patterns are highly evolvable. Though a mix of ecological drivers and speciation mechanisms likely influence the persistence of color patterns, our findings support the expectations for visually disruptive and communicative functions influencing the macroevolution of bold color patterns across teleost fishes. However, fishes are a highly diverse clade with a wide diversity of color patterns, so this is just the beginning of fish studies providing fruitful explorations of animal color and color pattern persistence (Salis et al. 2019).

CHAPTER 2

Correlated Evolution of Bold Color Patterns and Body Shape

INTRODUCTION

Bold color markings, made up of various pattern types, including bars, stripes, and blotches, are among the most eye-catching displays in nature. These high contrast patterns are used in communication (Hailman 1977; Cuthill et al. 2017) and may serve as anti-detection strategies (Stevens 2007). One way for animals to remain cryptic is to match the brightness, color, and pattern of the surrounding environment. This background matching strategy works exceptionally well if the animal is still. However, many species must move to go about essential functions, and thus 'break camouflage', making them detectable (Hailman 1977). Bold color patterns may offer an alternative. While they don't prevent detection, they may thwart or delay recognition even if movement is detected (Hall et al. 2013). Disruptive color patterns are characterized by high contrasting color margins within or across the animal's form and create visual contours that distract from an easily recognizable body outline (Cott 1940; Stevens and Merilaita 2009b). Termed disruptive coloration, this idea has gained considerable attention as an effective anti-recognition strategy (Cuthill and Székely 2009; Stevens and Merilaita 2009b, 2011; Tan et al. 2017) and may influence evolution of color patterns, especially in complex habitats

where the body pattern at least partially matched the background complexity (Phillips et al. 2017; van Niekerk and Mandiwana-Neudani 2018).

A subset of disruptive patterns, specifically repeating bars, stripes, and zigzags, may serve a separate anti-predator function (Stevens et al. 2008, 2011). These dazzle patterns are hypothesized to alter the viewer's perception of speed and directions of a moving object (Thayer and Thayer 1909). Since accurate hits are often required for prey capture, these dazzle patterns may prevent accurate tracking, helping prey avoid successful predator strikes (von Helversen et al. 2013). Two mechanisms are proposed to be responsible for the illusions: 1) the wagon wheel effect, which causes a viewer with visual processing slower than the pattern speed to see misleading snapshots of the pattern, much like watching the spokes on a wagon wheel appear to move in reverse, and 2) the barber pole illusion, which distorts direction via the aperture effect. Termed motion dazzle, bar, stripe, and zigzag patterns have experienced increasing attention within recent decades, though how much distortion is due to a dazzle-patterned individual in motion versus a group remains unclear (Hogan et al. 2016a). Several studies focus on human 'predators' reacting to targets on a computer screen, and suggest that multiple stripes in particular are difficult to accurately track while moving (Hughes et al. 2014, 2017,Hogan et al. 2016b). Some studies in smaller groups of animal taxa have helped test this strategy. Since the erroneous visual effect relies on movement, animals who are more active are thought to be most likely to display dazzle patterns. Indeed lizards with stripes

(rostro-caudal oriented patterns) were found to be more active foragers when compared to their cryptic counterparts (Halperin et al. 2017). Still, other findings suggest stripes and interrupted patterns are equally easy for human predators to 'catch', although both patterned targets were still harder to catch than uniform colored targets (Hämäläinen et al. 2015). It is important to recognize that, while dazzle patterns are included in the definition of disruptive patterns, the two functions are distinct strategies (Stevens et al. 2011).

Patterns are naturally restricted to the display surface that is an animal's body and some color patterns, such as repeating bars and stripes, can alter visual signals and create false perceptions of size and shape (Thompson and Mikellidou 2011). However it's not known if visual disruption and motion dazzle patterns may be more or less effective depending on body shape. Early work within fishes observed the angle of stripes and bars on the head corresponded to body shape and forehead slope in fishes: vertical bars were associated with deeper bodies and steeper foreheads, while the opposite relationship was found for horizontal stripes (Barlow 1972). Barlow hypothesized that high contrasting color margins may follow the primary margins of the body outline and might explain why barred fishes may have deeper bodies while striped fishes appeared more elongated. However, Barlow's observed relationship may also be driven by shared evolutionary history. We find the occurrence of bar and stripe patterns are more clustered on the phylogeny than expected under a random model of evolution (See Chapter 1) and body

shape is also expected to be more similar among closely related species. Since phylogenetic clustering of both pattern and body shape can result from shared ancestry, it is necessary to investigate whether there is a relationship between body shape and color pattern type using phylogenetic comparative methods which account for shared evolutionary history.

Fishes display repeating contrast bar and stripe patterns and a myriad of body shapes and are thus an excellent system within which to explore the relationship between pattern and body form. Biomechanical models connect fish body shape to locomotion, indicating shape can provide a useful proxy for how fishes move (Sfakiotakis et al. 1999). Fusiform shapes (streamlined, bullet-shaped forms) are most efficient for prolonged forward motion in a single direction at a steady speed (Webb 1994; Blake 2004) and thus will likely display any one patterned surface more consistently to a viewer. In contrast, deep bodied laterally compressed forms are more maneuverable, enabling rapid changes in direction and velocity (Langerhans and Reznick 2009) and it may be possible for these fish to 'flash' lateral color patterns as they maneuver in the water column. Though no specified movement is connected to dazzle effects, stripes are associated with linear flight strategies. Since striped animals are known to flee in the same orientation as their stripe patterns (Rojas 2017; Murali et al. 2018), and the majority of fishes move forward in the water column, we expect striped species to have more streamlined (and thus more straight-swimming forms) than fishes with bars, which may use more maneuverable

escape strategies (Rojas 2017). We also must take caution and recognize that body shape is known to provide other anti-predator functions apart from dazzle which may lead to coevolutionary relationships: deep bodies can limit predation by exceeding predator gape (Brönmark and Miner 1992) and aid in rapid c start escapes (Domenici and Blake 1997). These two functions may combine with dazzle coloration to influence the body depth of fish species.

Much of the literature on dazzle patterns has focused on computer 'capture' trials with human predators (Hughes et al. 2015, 2017,Hogan et al. 2016b) and it remains challenging to parse patterns found in nature into 'visual disruption' or 'motion dazzle' categories. Studies concerning the function of animal patterns and how those functions may influence the evolution of patterns have been mostly limited to smaller clades with clear pattern categories. We use a phylogenetic comparative framework to investigate evolutionary linkages between pattern and body shape across teleosts. Specifically, we ask the following questions: Do bars coevolve with deeper bodies and stripes with more elongate bodies, consistent with Barlow's observations? Or do we find species with bars and stripes have evolved similar body shapes to each other, but differ from body shapes of species without bar or stripe patterns, consistent with the expectations of motion dazzle?

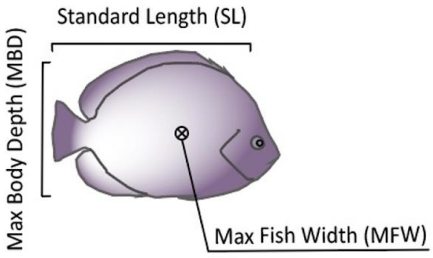
METHODS

Pattern data

We used the presence/absence scores for 14 pattern types from photographed museum specimens representing over 6000 species of teleost fishes from Chapter 1.

Body shape data

To quantify the overall shape of the lateral surface of the fish I used standard length (SL) and maximum body depth (MBD). We also included maximum fish width (MFW) as a control, as it is the other major size axis but is not the surface on which the patterns were scored. The measurements were taken with calipers on adult sized specimens at the Smithsonian museum and form a subset of the teleost body shape morphospace of (Price et al. 2019b). These measurements were taken on the same specimens that were photographed and used to categorize pattern, however not all photographs were suitable leaving us with 5171 species in the analyses. To separate size from shape we size-corrected the traits using log shape ratios with size estimated as the geometric mean of SL, MBD and MFW. For further details concerning the shape data see(Price et al. 2019b).



Size (geometric mean) = $\sqrt[3]{(SL)(MBD)(MFW)}$

Figure 1: Morphological measurements were recorded for three museum specimens per species to determine fish size and shape. Linear measurement data was used to calculate geometric means (size).

Phylogenetic ANOVAS

We employed phylogenetic ANOVAS (Garland et al. 1993) to test whether boldly patterned fishes have distinct shapes relative to fishes that have no pattern or have patterns that are not bold e.g. mottling (hereafter referred to collectively as non-contrast patterns). Multiple pairwise tests were run for the three size-corrected measures (SL, MBD & MFW): 1) multiple plus single bars vs non-contrast patterns, 2) multiple plus single stripes vs non-contrast patterns, and 3) non-bar or stripe contrast patterns (e.g. reticulate or blotched patterns) vs non-contrast patterns. To test if fishes with dazzle patterns (such as repeating bar or stripe) differed in shape from those with other contrast patterns (bold patterns that don't repeat such as a single stripe), I also ran a phylogenetic ANOVA comparing the three shape traits between single and multiple stripe species. An equivalent analysis within bar traits was prevented by the low number of single barred species (20 species). As we have found that bold color patterns are more commonly found in reef fishes (see Chapter 1) and previous work using our body shape dataset

identified that reef-associated species have deeper more maneuverable shapes than marine species in other less complex habitats (Larouche et al. 2020). I also ran analyses only within the reef-associated fishes identified by Larouche et al. Due to the low number of single bar species and differences in body shape found in single stripe and multiple stripe fishes within teleosts, we narrowed our comparisons to multiple stripe and multiple bar species. Comparisons for the three axes of size-corrected body shape were done for the following pattern combinations within reef fishes: 1) multiple bars vs non-contrast patterns, 2) multiple stripes vs non-contrast patterns, 3) multiple bars vs multiple stripes, and 4) multiple vs single stripes.

RESULTS

Within teleosts, species with either a single or multiple bar have shorter standard lengths and deeper bodies than species with non-contrast patterns (Figure 2 a-b) but there was no significant difference in shape between multiple or single striped fishes and non-contrast pattern fishes (Figure 2 d-f). Similarly, when non-contrast pattern species were compared to species with contrast patterns that are neither bars nor stripes, we find no significant shape differences (Figure 2 g-i). However, interestingly single stripe teleosts have longer standard lengths and less deep bodies than multiple stripe species (Figure 2 j-l).

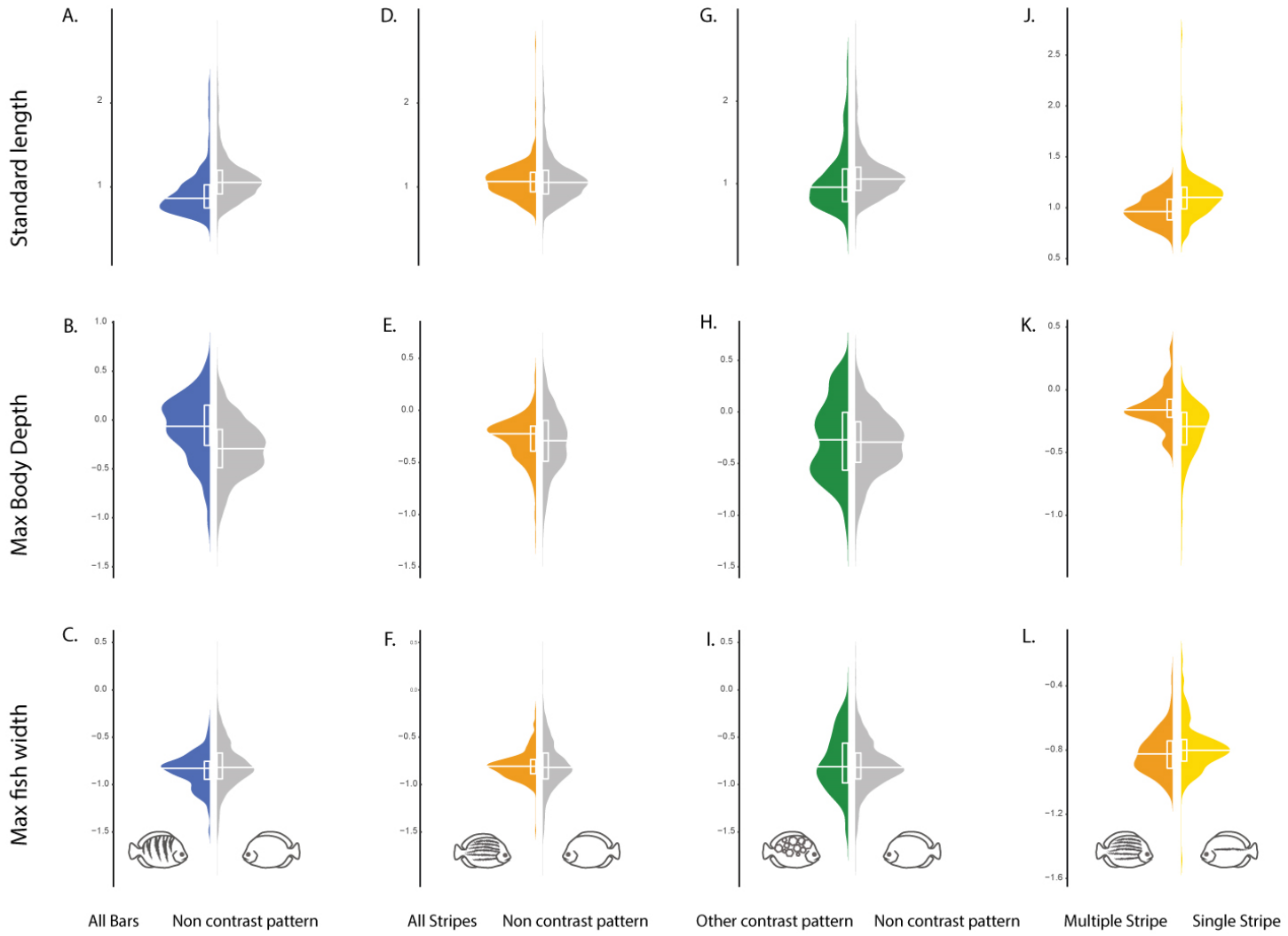


Figure 2: Distribution comparisons of teleost species with color pattern type presence versus absence.

TELEOSTS		Categories compared	adj R^2	p value	given phylogeny
	SL	All bar vs non CP	0.0185	< 0.05	< 0.05
		All stripe vs non CP	0.0004	0.09	0.58
		Other CP vs non CP	0.0009	< 0.05	0.24
		Single vs Multiple stripe	0.1007	< 0.05	0.07
	MBD	All bar vs non CP	0.0279	< 0.05	< 0.05
		All stripe vs non CP	0.0002	0.15	0.61
		Other CP vs non CP	0.0004	0.10	0.62
		Single vs Multiple stripe	0.1536	< 0.05	< 0.05
	MFW	All bar vs non CP	0.0019	< 0.05	0.40
		All stripe vs non CP	-0.0002	0.80	0.93
		Other CP vs non CP	0.0006	0.06	0.52
		Single vs Multiple stripe	0.0095	0.06	0.60

Table 1: Phylogenetic ANOVA results for relationships between body shape variables and pattern trait combinations (See Figure 1) for teleosts.

Reef fishes with multiple bars had more maneuverable body shapes with shorter standard lengths and deeper bodies than non-contrast patterned species (Figure 3, Table 2). However, we find no difference in body shape for multiple stripe species compared to non-contrast patterned species. Although it should be noted that the number of reef fishes with multiple bars (121 species) far exceeds the number with multiple stripes (51 species). When multiple bar fishes were compared to multiple stripe fishes, we see a clear difference in body depth between the two groups with barred fishes being deeper bodied (see Figure 3) but this relationship is not significant when phylogenetic relationships are taken into account (see Table 2).

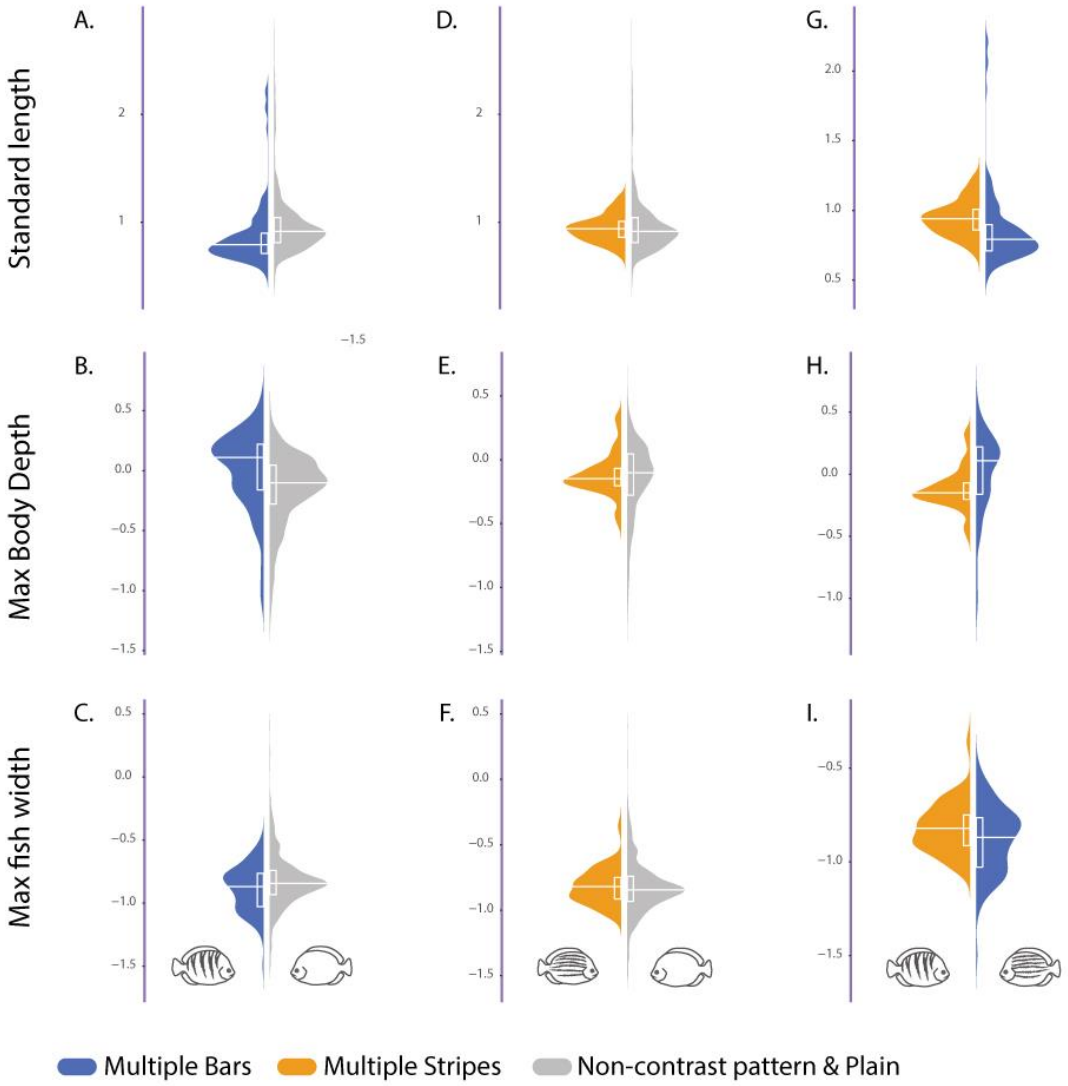


Figure 3: Distribution comparisons of reef species with color pattern type presence versus absence.

REEF FISHES		Categories compared	adj R^2	p value	given phylogeny
	SL	Multiple bar vs non CP	0.0118	<0.05	<0.05
		Multiple stripe vs non CP	-0.0003	0.3933	0.61
		Multiple bar vs Multiple stripe	0.0093	0.1094	0.43
	MBD	Multiple bar vs non CP	0.02914	1.738e-08	<0.05
		Multiple stripe vs non CP	-0.0003	0.414	0.63
		Multiple bar vs Multiple stripe	0.0360	0.007372	0.15
	MFW	Multiple bar vs non CP	0.0068	0.004392	0.14
		Multiple stripe vs non CP	-0.0010	0.9401	0.97
		Multiple bar vs Multiple stripe	0.0198	0.03666	0.29

Table 2: Phylogenetic ANOVA results for relationships between body shape variables and pattern trait combinations (See Figure 1) for reef fishes.

DISCUSSION

I find species with single or multiple bars have deeper, more maneuverable body shapes than those without contrasting patterns. Despite reef fishes having more maneuverable, deep bodied shapes than non-reef marine species (Larouche et al. 2020), I find the same association between deep bodied, shorter forms and contrasting bar color patterns within reef fishes, indicating support for correlated evolution of maneuverable shape and bar patterns independent of the influence of complex habitats. In contrast, I did not find a significant association between body shape and the presence of stripes, indicating that bar and stripe patterns may experience differing evolutionary pressures over this timescale. While deep body shapes coevolving with bars correlates with Barlow's expectations when accounting for phylogeny, the lack of body shape differences in stripe fishes compared to non contrast patterned fishes runs contrary to the expectation of streamlined, elongate fishes using stripes as shape disruption (Barlow 1972). However, I find a difference in body shapes between single and multiple striped fishes in teleosts and reef species, which may indicate that singular and repeating patterns function differently, leading to contrasting relationships between pattern and body shape.Although it should be noted that single stripe and multiple stripe fishes did not show a shape difference when compared to non contrast pattern fishes separately. While these findings are not entirely consistent with Barlow's observations: striped fishes do not show a correlation with elongated shapes, it is important to not interpret this as not supporting the disruptive

function of these patterns, as shape disruption can be achieved by a variety of bold color pattern orientations in other systems (Cott 1940).

Deeper body shapes have been associated with enhanced swimming maneuverability and increased fast-start performance, as the kinematics and mechanics of turns and fast-starts are similar (Blake 2004). I find barred and striped species are deeper bodied than non-contrast patterned species, indicating that these repeating patterns may coevolve with a movement strategy. Motion dazzle may be influencing the body shape of species with multiple stripes or bars, as dazzle requires motion to create illusions and most fishes use fast-starts to escape predators, which are enhanced by deeper bodies. There is still discussion on what types of motion are needed to have illusory effects, and if dazzle requires high speeds (Scott-Samuel et al. 2011). Background distractors, such as other dazzle-patterned animals in a moving group, may provide additional illusions - this is one of the prevailing hypotheses behind zebra stripes (How and Zanker 2014). Other studies distinguish between linear movement, associated with stripe patterns, with more irregular maneuvers, associated with non-linear patterns (Rojas 2017). Perhaps some of the difficulty in distinguishing ‘dazzle movement’ and ‘dazzle patterns’ may lie in the multifunctional nature of some color patterns, as has been suggested by study in vipers (Valkonen et al. 2020). However, tests with moving targets on computer screens indicate camouflage and motion dazzle may not be complimentary (Stevens et al. 2011).

Both across teleosts and within reef fishes, species with single stripes had more elongate, less maneuverable body shapes than the multiple stripe fishes, supporting different swimming strategies for single or multiple patterned fishes. While both single and multiple stripe patterns could disrupt body shape, the streamlined, steady swimming shapes found to coevolve with single stripes suggests they may aid in linear escape. Single stripes in particular may have special significance for signaling specifically antagonistic interactions such as competition over territory and in reef fishes. Cleaning species eat parasites off of others, providing a service at specific locations in reef habitats and often have a bold lateral stripe (Stummer et al. 2004; Arnal et al. 2006). This signal is thought to be an advertisement for the parasite removal and many cleaner species sport similar striped color patterns (Stummer et al. 2004). However, we also found that single stripes are more common in freshwater habitats (see Chapter 1) where cleaning behavior is unknown.

While the patterns we have found hint at some exciting possibilities, there is still much to be investigated before we can tease apart the potential impacts of shape-disruptive camouflage and motion dazzle. Vision in aquatic environments can be variable. Turbidity and light attenuation can cause visual acuity to degrade and change the perception of patterns that appear bold to the human eye (Marshall et al. 2019). Different light colors are filtered out depending on depth, and both reef, open water, and freshwater lakes and rivers can become murky with suspended particulates, obstructing clear views of pattern boundaries. It is also important to consider the receiver of visual signals. While some predators may be thwarted by dazzle patterns, others with better visual capabilities may

not have difficulty capturing dazzle-patterned prey, even at higher speeds. For example, viper patterns may prevent successful attacks from mammalian predators but not raptors (Hämäläinen et al. 2015; Zlotnik et al. 2018; Valkonen et al. 2020). In addition to predator acuity, capture strategy may also influence the effectiveness of predation attacks; while many land predators make contact with a portion of the prey's body, aquatic predators can attack from anywhere within a three-dimensional environment to engulf prey by ram or suction feeding. Continued work on the visual capabilities of aquatic animals can help distinguish which color patterns may be cryptic or conspicuous given these conditions.

CONCLUSION

Our study is the first to investigate the correlated evolution of pattern types and body shape across a large clade. We uncover significant relationships between bold color patterns and body shape, indicating they have co-evolved. Motion dazzle may be the only function that is consistent with all our findings, as both multiple bar and multiple stripe fishes have deeper, more maneuverable bodies that are likely better at escaping predators through fast-starts. However, much more research is needed at both microevolutionary and macroevolutionary scales to determine if the evolutionary patterns found are due to phylogenetic inertia or consistent selection, in addition to assessing the types of movement responsible for illusions of speed and direction. This work is the first step

towards understanding the evolution of the awe-inspiring diversity of bold color patterns within fishes, and reef fishes in particular.

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